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Fast and massive settlement of boring bivalves on coral slabs at Taboga Islands, Eastern Pacific, Panama

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Abstract

Hundreds of natural recruits were observed on coral slabs exposed for five to six months at Urabá Island, Taboga Islands, Eastern Pacific in the course of experiments with chemically boring bivalves. Based on the size range of the specimens, the recruitment was a very fast phenomenon where many settled probably within days, many more during the following weeks. Recruits of the most common species, the mytilid *Lithophaga (Leiosolenus) aristata* (Dillwyn, 1817), reached up to 16.3 mm in length after 165 days during "winter" experiments. Densities of up to 5 borehole orifices per cm^2 were found. These results strongly contrast with results from previous recruitment experiments conducted in the tropical waters of the northern Red Sea, the Australian Great Barrier Reef and French Polynesia. Differences in recruitment on experimentally exposed substrates and possible reasons for the fast and intense settlement of boring bivalves at Urabá Island are discussed. For the latter, firstly the generally high organic turnover rate, and secondly the larval abundance of boring bivalves at the beginning of experiments appear to be largely responsible for the results.

Key Words

Bioerosion, corals, bivalves, recruitment, *Lithophaga*, E Pacific.

Riassunto

Centinaia di colonizzazioni sono state osservate su lastre ottenute da colonie di coralli esposte per un periodo compreso tra cinque e sei mesi nelle acque dell'Isola di Urabá, presso le Isole Taboga (Pacifico orientale), nel corso di esperimenti su bivalvi perforanti con modalità chimica. Sulla base delle dimensioni degli esemplari, la colonizzazione risulta essere stata molto veloce, con molte larve che si sono impiantate entro pochi giorni, e molte di più durante le settimane successive. La specie più comune, il mitilide *Lithophaga (Leiosolenus) aristata* (Dillwyn, 1817), ha raggiunto una dimensione massima di 16,3 mm di lunghezza dopo 165 giorni, durante la fase sperimentale "invernale". Per i bivalvi perforanti, è stata riscontrata una densità massima pari a 5 perforazioni per cm^2. Questi risultati contrastano fortemente con quelli ottenuti da precedenti esperimenti di colonizzazione naturale condotti nelle acque tropicali del Mar Rosso settentrionale, della Grande Barriera Australiana e della Polinesia Francese. Vengono discusse le differenze nella colonizzazione di substrati esposti sperimentalmente e i possibili motivi della veloce ed intensa colonizzazione da parte di bivalvi perforanti nelle acque dell'Isola di Urabá. I motivi sembrano soprattutto rappresentati da un tasso di *turnover* organico generalmente alto, e abbondanza di larve di bivalvi perforanti nell'area investigata.

Parole chiave

Bioerosione, coralli, bivalvi, colonizzazione, *Lithophaga*, Pacifico orientale.

Introduction

Since the early publication of the extensive and annotated bibliography on marine borers by Clapp & Kenk (1963), one main focus of interest by the scientific community has been their influence in reef habitats. In such a perspective Neumann (1966) introduced the term bioerosion in his study of boring sponges, expanding the process to include abrasion by grazers as well. A first comprehensive review on the destructive action of coral reefs by organisms (Hutchings 1986) was further implemented by the bibliographic overview of micro- and macroscopic bioerosion (Radtke et al., 1997), and, more recently by the study of Wisshak & Tapanila (2008, and references therein).

Research on micro- and macro-borers covers a wide range of recent and fossil situations. Apart from studies focussed upon certain groups or genera and species of bioeroders, increasing interest has been devoted to their life-cycle and co-occurrence, including succession rates and inter-specific competition. Field experiments were conducted with exposed substrates in various designs for micro- and/or macroborers. Microborers, such as bacteria, fungi and cyanophytes, can already be observed in carbonate substrates after a few days or weeks of exposition (Radtke et al., 1996, 1997; Vogel et al., 1996, 2000; Gektidis 1999; Tribollet et al., 2002; Tribollet & Golubic, 2005). Macro-borers, such as polychaetes, sponges and bivalves, generally colonize freshly available substrates later (Hutchings, 1981, 2008; Hutchings & Murray, 1982; Hutchings & Bamber, 1985; Kiene & Hutchings, 1985, 1994; Hutchings & Peyrot-Clausade, 1989, 2002; Hutchings et al., 1992; Peyrot-Clausade et al., 1995; Pari et al., 1998, 2002).

Within the community of borers, individual succession rates and times of reproduction and settling on available substrates greatly influence the sequence of borers and their composition in early and "mature" communities. This raises key questions such as: which species will be pioneers and what interactions will follow, which will succeed and potentially dominate colonisation and "mature" communities, which will have the greatest impact on the boring process.

In bivalves, successful settlement was recorded after two or three years and only in very low numbers in experiments conducted at the Australian Great Barrier Reef (Hutchings, 1981; Hutchings & Murray, 1982; Hutchings & Bamber, 1985; Kiene & Hutchings, 1985; Sammarco & Risk, 1990; Tribollet et al., 2002; Tribollet & Golubic, 2005), in French Polynesia (Pari et al., 2002), and in the northern Red Sea (Hassan, 1998). Nevertheless, results in bioerosion intensity can differ considerably according to geographical location, season and food supply conditions (Highsmith, 1981, 1983; Hallock, 1988; Scott et al., 1989; Sammarco & Risk, 1990; Hutchings et al, 1992; Tribolett et al., 2002). Kleemann (1990) reported on the growth and boring rates of bivalves inserted in coral slabs and mentioned only briefly the presence of natural recruits. The present article focuses on the latter and provides evidence for a very fast, numerous and successful settlement of lithophagine bivalves. Being in striking contrast to earlier results, this recruitment is discussed and probable hypotheses forwarded.

Material and methods

Zooxanthellate scleractinians, mainly *Siderastrea siderea* (Ellis & Solander, 1786), were collected from Caribbean coral reefs on two occasions by snorkelling in front of the breakwater at Fort Randolph, Colón, Panama. The Atlantic side was chosen because no suitable substrates could be obtained on the Pacific side. Carbonate substrates occurring near the Naos laboratory of the US Smithsonian Institution and at Taboga Islands proved to be already heavily infested and eroded by borers. The sampled corals were transported still wet back to the Naos laboratory the following day (by train: Nov. 1981), or the same day (by car: May 1982), for further treatment. 3.5 to 7-cm-thick slabs were cut using a hand saw from the coral heads. Once in the laboratory, young boring bivalves, by large belonging to lithophagine mussels, were placed into closely fitting, previously drilled and measured artificial holes in the slabs (Kleemann, 1990). After a few days in tanks with running seawater, the inserted bivalves usually had secreted a new byssus functional to their internal stabilization, and thus facilitating their further handling. The slabs were fastened inside mesh-wire cages which were shipped to the wreck at Urabá Island's East coast and firmly attached inside the iron hull in 1-2 m depth at low tide (Kleemann, 1990: fig. 3). In most cases, the natural upper side of the slabs was oriented up and only exceptionally upside down to save space. The cut sides, facing sideways, were relatively smooth and typically nearly upright in orientation during exposure. The sides with inserted bivalves were oriented toward the centre of the mesh-wire cages. The mesh width, 11-12 mm in diameter, was chosen to keep off larger potential predators such as fish and crabs. The cages also facilitated transport and attachment of the experimental material inside the wreck.

Experiments were performed in two seasons. In the "winter" experiments, corals were brought into the field in two parts on 5 and 9 Nov. 1981, containing 302 and 328 bivalves respectively. Cages with coral slabs were recollected on 17 and 20 April 1982 and had been exposed for 165 respectively 163 days. They were examined first superficially and cleaned by scratching off most of the fouling organisms. This yielded a better view from all sides and of the superficial boring traces. The slabs were then carefully split into pieces with hammer and "slit"-chisel for detailed investigation. In the "summer" experiments, new coral slabs, either free of or with inserted bivalves, and some old coral fragments were exposed for 174 days, from 10 May to 1 Nov. 1982.

Results

The recollected mesh-wire cages were partly covered by a dense variety of fouling organisms, as were the slabs inside. The latter had to be cleaned of the larger foulers, including bryozoans, sedentary polychaetes, cirripeds and oysters, by brushing and scraping. This procedure also revealed an intense settlement by veligers (larvae) of boring bivalves during the "winter" experiments. This was evident in the development of numerous boreholes of juvenile lithophagines, corresponding to dozens of recruits per coral slab (**Figs 1-5**). The most common bivalve species was *Lithophaga (Leiosolenus) aristata* (Dillwyn, 1817); in addition several *L. (Leiosolenus) plumula* (Hanley, 1843) and a few recruits of *L. (Leiosolenus) attenuata* (Deshayes, 1836) were also identified (Kleemann, 1986a). A wide size range was particularly evident in the dominating *L. aristata* recruits, where shell length varied from about 2-16 mm after maximally 165 days (**Figs 1, 3B**). Many recruits had grown so fast, reaching a maximal shell length of 16.3 mm, that several specimens could be used in the follow-up "summer" experiments to gain more boring and growth rates (Kleemann, 1990).

The coral tissue of the first three slabs, cut and implanted with boring bivalves, survived both the above-mentioned handling and exposure process. The coral tissue had spread a few millimetres onto the cut sides. The living tissue prevented any settlement by veligers of dead-coral boring lithophagine species there (see discussion). In later prepared slabs, coral tissue did not survive. The tissue of the individual slabs that did not

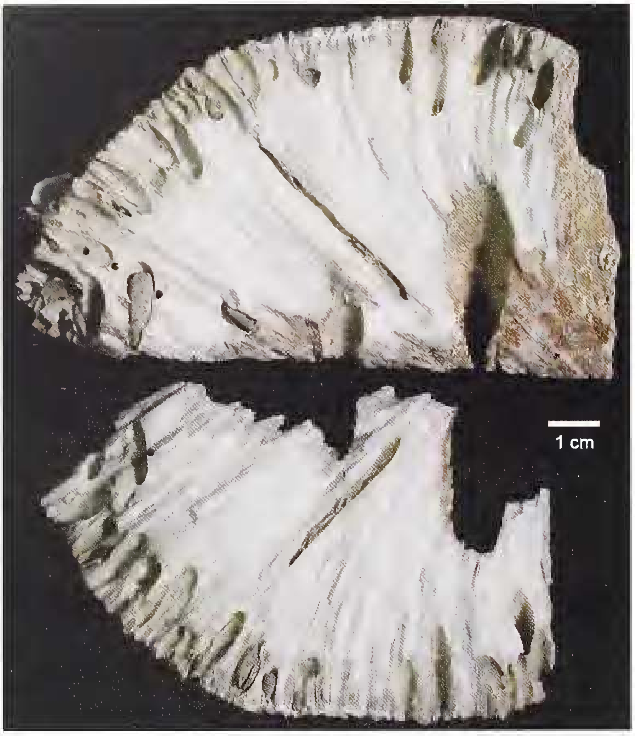

Fig. 1. *Siderastrea siderea*. Split open to exhibit the many boreholes and recruits of *L. (Leiosolenus) aristata* along the curved outline of the coral. Their wide range in length demonstrates repeated spatfall during a prolonged settling season in "winter" (beyond individual differences in post-settlement growth). Four polychaete borings are also visible: centrally one fairly straight and deeply penetrating boring, plus three cross sections, about 2 mm in diameter, on the left. Photo C. Baal.

Fig. 1. *Siderastrea siderea*. Superficie di frattura mostrante molte perforazioni e colonizzazioni da parte di *L. (Leiosolenus) aristata* visibili lungo il contorno della colonia. L'ampia variabilità in dimensioni dimostra ripetuti impianti di larve durante l'intero periodo "invernale" dell'esperimento (oltre a differenze nell'accrescimento successivo all'impianto). Sono visibili anche quattro perforazioni da policheti: al centro, una perforazione piuttosto rettilinea e molto profonda, assieme ad altre tre, a sinistra, con sezione di circa 2 mm. Foto C. Baal.

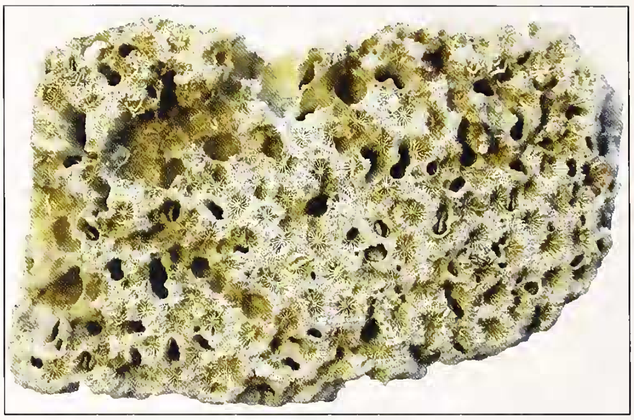

Fig. 2. *Siderastrea siderea*. Fragment in top view, 6 x 4 cm. The former "natural" surface structure is pitted by many, variously wide orifices and eroded boreholes of mainly *L. aristata*, indicating repetitive settlement of recruits, mostly during "winter". Photo K. Kleemann.

Fig. 2. *Siderastrea siderea*. Superficie superiore di un frammento di dimensioni 6 x 4 cm. La superficie "naturale" della colonia presenta molte perforazioni, di varie dimensioni, in prevalenza da parte di *L. aristata*, indicative di ripetuti impianti di larve in gran parte avvenuti durante la fase "invernale". Foto K. Kleemann.

survive probably died early on after exposure to air before being returned into seawater. The effects the decaying coral tissue on the beginning of colonisation and succession of settlers remain unknown.

Except for the first three slabs, new borings were dominantly situated on the previously live surfaces. In *S. siderea*, this surface normally consists of 3-4 mm wide, shallow calices, filled with densely packed, narrow and fine-grained septa (**Figs 2, 3A, 5A**).

Aggregations of more than five borehole orifices per cm^2 were often recorded on other natural surfaces and occasionally occurred on the cut sides of the slabs as well. On the latter, they were mainly situated near the edges towards the natural surface (**Fig. 4**). Generally, borings in the cut sides of *Siderastrea* were fewer but still common (**Figs 4, 5D**).

While numerous new orifices of bivalve boreholes were found in the slabs after the "winter" experiments, much fewer new borings and only very young or small recruits were found after "summer" (see discussion, **Fig. 5A-D**).

A single recruit of a boring crenellid bivalve, *Gregariella coarctata* (Carpenter, 1856), was also found (Kleemann, 1986b). The specimen measured 6.7-3.6-2.8 mm in length-width-height; its borehole depth was 8.7 mm and the borehole aperture 2 mm wide. For comparison: during the same time, three inserted *G. coarctata* specimens had grown 5.2 mm in length from 7.9 to 13.1 mm; 5.5 mm from 11.7 to 17.2 mm; and 1.4 mm from 18.6 to 20.0 mm respectively.

Discussion

In recent decades, several field experiments were conducted to analyse the contribution of marine borers in the erosional processes of coral reefs and to assess the balance between reef growth and decay. Exposing experimental substrates for different periods of time is one method to obtain results on colonisation, settlement, growth and boring rates as well as on the succession of various bioeroders. In such experiments, calcareous substrates of different origin and size were exposed in the field under different conditions. These conditions (locality, season, depth, etc.), depended on the respective (main) goal, e.g. assessing the amount of accretion versus erosion, general observations on the succession of micro- and/or macro-borers, or the study of specific abrading or boring organism groups.

For studying micro-borers, the experimental substrates can be small and are easily selected of various origin and texture, e.g., ooids (Gektidis, 1997), little pieces of Iceland spar crystals, mollusc shells and reef corals, often trimmed to about one or a few cm in largest dimension (Rützler & Rieger, 1973; Radtke et al., 1996; Vogel et al., 2000; Radtke & Golubic, 2005).

For macro-borer investigations, experimental substrates need to be larger, reducing the choice of suitable material. Several authors used rectangular blocks cut from live *Porites* in variable sizes, e.g., 7.5 x 5 x 1 cm (Davies & Hutchings, 1983), 5 x 5 x 8 cm and 10 x 10 x 2 cm

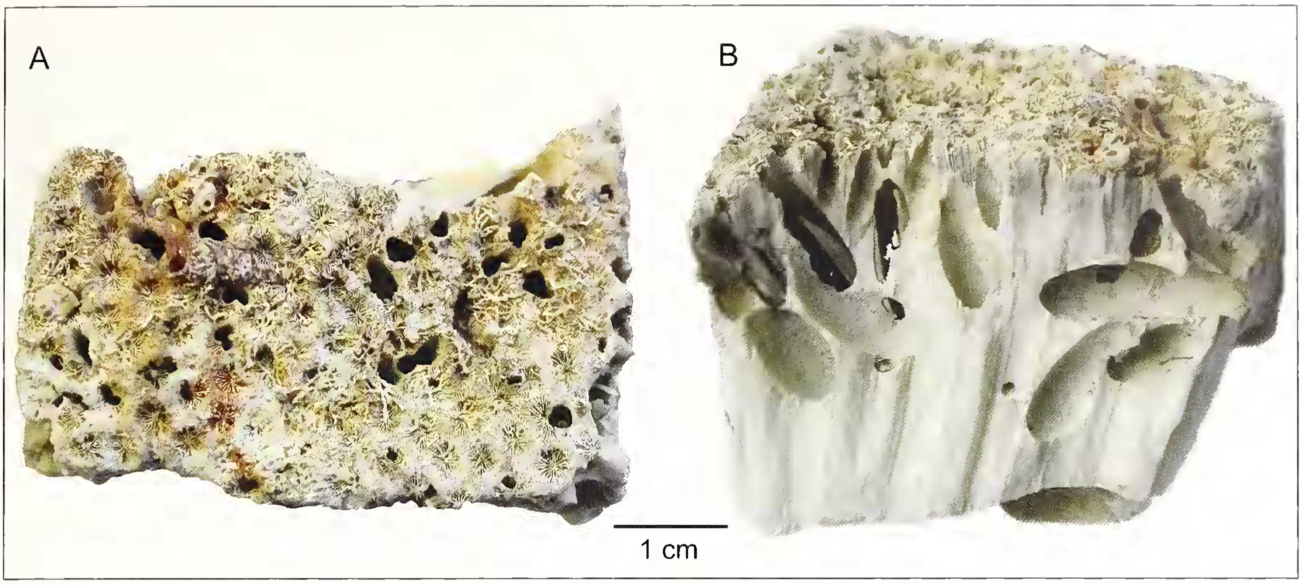

Fig. 3. *Siderastrea siderea*. **A.** Another fragment in top view, after removal of larger fouling organisms (many tiny and some bigger sedentary polychaete tubes remain). Note the density and the differing size of borehole orifices, figure-of-eight-shaped in *L. aristata* and round in *L. plumula*, two are situated in the right lower corner. Slab width (across) 53 mm. **B.** Same fragment as in Fig. 3A. The split open surface exhibits numerous borings of *L. aristata*, several intersecting in intra-specific space competition, aggregated at slab edges. A few polychaete borings in cross section are near the photo bottom. Photos K. Kleemann.

Fig. 3. *Siderastrea siderea*. **A.** Superficie superiore di un frammento dopo la rimozione degli organismi incrostanti più grandi (molti tubi di policheti sedentari di piccole dimensioni ed altri di maggiore taglia sono ancora in posto). Si noti l'elevata densità e le diverse dimensioni delle perforazioni, a forma di otto in *L. aristata* e circolari in *L. plumula*, due ubicate presso l'angolo inferiore destro. Ampiezza del campione 53 mm. **B.** Stesso frammento. La superficie di frattura mostra numerose perforazioni di *L. aristata*, alcune delle quali si intersecano in seguito a competizione intraspecifica per lo spazio. Sono presenti anche perforazioni da policheti (in sezione) nella parte inferiore. Foto K. Kleemann.

(Hutchings et al., 1992), 8 x 4 x 4 cm (Hutchings & Peyrot-Clausade, 2002), and 8 x 8 x 5 cm (Tribollet et al., 2002), 200-500 cm^3 (Kiene, 1985), or discs, 1 cm thick and 10 cm in diameter (Kiene, 1989). The experimental substrates are usually pristine in the beginning (Hutchings, 1981; Kiene, 1985; Hutchings & Peyrot-Clausade, 1989; Kiene & Hutchings, 1992; Chazottes et al., 1995; Hassan, 1998; Hutchings & Peyrot-Clausade, 2002; Hutchings & al., 2005; Osborne et al., 2005; Hutchings 2008). Substrates can be brought directly into contact with potential borers (Rützler & Rieger, 1973), or may already carry specimens of boring species (Kleemann, 1986b, 1990). In the present "winter" experiments, mainly live Caribbean *S. siderea* heads were chosen as a substrate for technical reasons. This was mainly because no suitable substrate was available for the experiments at the Pacific side (Urabá Island). There, only very few coral species were present, consisting of small patches of low growing *Pocillopora* thickets at about 2 m depth and a few massive *Pavona* and *Porites* colonies in about 5-7 m. Except the uppermost 10 cm below the live tissue in massive corals and the branch-tips of *Pocillopora*, all other carbonate substrates were already inhabited by various borers (Hutchings 1986) and strongly eroded. The live corals apparently grew only slightly faster than the rate with which they were being eroded from below. The borers probably consisted mainly of boring bivalves and sponges based on briefly lifting larger colonies from the sea floor by hand.

The eastern Pacific *Pavona* and *Porites* species serve as hosts for the associated *L. (Leiosolenus) laevigata* (Quoy & Gaimard, 1835; including *L. (Leiosolenus) hancocki* Soot-Ryen, 1955, and of later authors). Particularly *Porites* colonies were additionally riddled by *L. laevigata* bivalves from above (Kleemann 1982: fig. 9). Therefore, live corals were collected at the Caribbean side of Panama for the experiments. The chosen *S. siderea* colonies, somewhat flat-spherical or loaf-shaped, were abundant and big enough to be cut into ~5-7 cm thick slabs. Most showed no macro-borers, except on dead parts. One sample contained a single specimen of *L. (Leiosolenus) appendiculata* (Philippi, 1846) (= *Lithodomus bisulcata* Orbigny, 1853: Kleemann, 2009).

Recruitment of boring organisms takes place by larvae which settle on the substrate, metamorphose and quickly bore into it (Hutchings, 1986). Micro-borers usually play a role as pioneers of the endolithic community. Their activities facilitate and support the later settlement of macro-borers. The latter are generally handicapped by a seasonally restricted spawning period for reproduction and recruitment once a year. Distinct seasonality of recruitment has also been noted in polychaetes (Hutchings & Murray, 1992; Hutchings & Peyrot-Clausade, 2002). Several polychaete borings were found in the slabs (**Figs 1, 7**).

In the succession of borers in newly available substrates at Lizard Island, Australian Great Barrier Reef (GBR), polychaetes played an important role in the initial stages of bioerosion (Hutchings, 1981; Hutchings & Bamber, 1985). Kiene & Hutchings (1994) suggested that the age of the experimental substrates may strongly influence the nature of succession by macroborers and the suitability for further recruitment. In the present case, the coral blocks contained an artificial *Lithophaga*-community from the start of the "winter" experiments. The presence of these adults during the settling season may have triggered the prompt "invasion" of con-specifics and promoted the abundant and successful settlement of recruits. I hypothesise that coral-associated *Lithophaga* (Kleemann, 1977, 1980, 1982, 1995, 2008; Scott 1988a, b; Kleemann & Hoeksema, 2002; Kleemann & Maestrati, 2012) benefit if they can find their proper hosts actively based on chemical traits ("smell") and also if con-specifics are already present, providing a good chance for a successful maintenance of the population.

At Lizard Island, GBR, polychaetes were important in the early stages of bioerosion of newly available coral substrate. Particularly *Polydora* species recruited within three months and *Dodecaceria* species within three to six months of exposure, probably facilitating subsequent recruitment by the sponges, sipunculans and molluscs that dominate 'mature' boring communities (Hutchings, 2008). Recruitment of boring polychaetes varies according to the type of substrate available, season and geographical location, along with environmental factors such as light, water quality, depth, and wave exposure (Hutchings, 2008). These factors may influence bivalve recruits as well. Generally, any broader interpretations of local results from bioerosion studies must be undertaken with caution.

Although polychaetes also recruited in the present experiments at Urabá Island, Taboga Islands (**Figs 1, 7**), lithophagine bivalves were the dominant settlers of the boring community and apparently preferred upper surfaces. The previously live coral surface of the exposed slabs appeared to be most attractive to the veligers (**Figs 1-3, 5**), followed by an adjacent narrow part on the cut sides (**Fig. 4**). The surface structure of the sides themselves was rather smooth and thus probably less attractive, providing fewer niches to settle. Beyond the orientation of the surfaces, the direction and velocity of the larvae-carrying water flow may also play a significant role in settlement results (Seilacher, 1969).

Spatfall at Urabá Island was high, particularly by *L. aristata*, of which a remarkable number survived for at least several weeks to months. This recruitment and survival took place despite strong space competition by mainly fouling and encrusting organisms along with a few other endozoans. The latter included related *L. plumula* and *L. attenuata* as well as unidentified polychaetes.

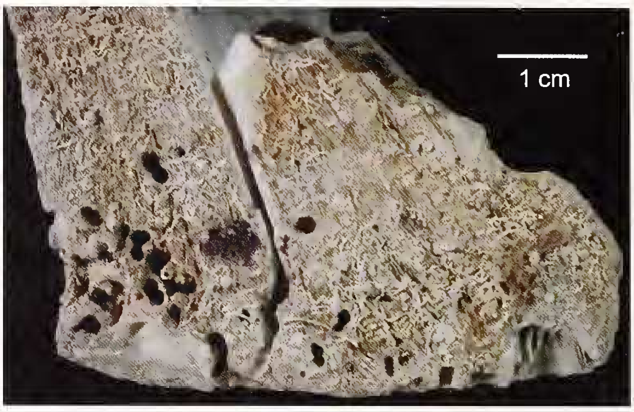

Fig. 4. *Siderastrea siderea*. New *L. aristata* borehole openings, aggregated on the cut side, near the natural coral surface (at bottom). Larger epifauna, e.g., cirripeds and tunicates, were scraped away, over one hundred tiny tubes of sedentary polychaetes remain. Photo C. Baal.

Fig. 4. *Siderastrea siderea*. Nuove perforazioni da parte di *L. aristata* concentrate presso il margine della sezione, vicino alla superficie naturale della colonia (in basso). L'epifauna di maggiori dimensioni, quali cirripedi e tunicati, è stata asportata, mentre circa un centinaio di sottili tubi di policheti sedentari sono ancora presenti. Photo C. Baal.

The natural coral surface structure appeared to be more frequently chosen and penetrated than the hand-saw cut sides. The small orifices of bivalve recruits, apart from the artificial boreholes, were detectable only after removing the fouling organisms from the slabs. Settling veligers of boring bivalves were no doubt hindered by this epifaunal space competition, e.g., oysters reaching up to 40 mm in diameter at the end of "summer" exposure (**Fig. 6**). Overgrowth and closure of already existing boreholes did occur, whereby larger boring bivalves sometimes managed to keep their borehole orifices open with their siphons. The dense aggregations of fouling and encrusting organisms and their rapid growth point to a high organic turnover rate at Taboga Islands. This may reflect up-welling in the Eastern Pacific, which seemed particularly intense at Urabá Island.

In principle, local larval abundance should correspond with the local population of adults. Local *L. aristata*, the most common dead-coral boring bivalve, and probably other lithophagine species have an extended settling period, presumably starting already in October. Accordingly, "winter" experiments were colonized immediately over a period of several weeks, as indicated by the size range of recruits (**Figs 1, 3B**). "Summer" experiments displayed a sensibly lower infestation by lithophagine recruits and, considering their small size, most likely only in the last month, October 1982. A simultaneous, coincidental or brief settlement and undisturbed development of young bivalves should yield a single and narrow size group. Prolonged settlement or, less likely, repeated spatfall over a year will yield a much wider size range of recruits of the same year.

During a parallel study on the settling preferences of Eastern Pacific dead-coral boring bivalves in the "summer" experiments, I added uninhabited blocks of various coral texture (apart those with inserted specimens). This was designed to determine the influence of skeletal structure (Kleemann, 1990). Unfortunately, too few recruits were found after the "summer" period for a more detailed analysis but this attempt did provide further proof of bivalve settlement at least within weeks to a few months on newly available substrates. The seasonal influence on *L. aristata* recruitment was striking. Considering the wide size rage of its recruits after the "winter" period, a very prolonged settling season can be assumed at least for this species. I consider that the size differences in the recruits mainly reflect the varying available amount of time after metamorphosis and less the micro-environmental parameters (food and space competition). Several *L. aristata* recruits had grown so fast that they could be used in the follow-up "summer"

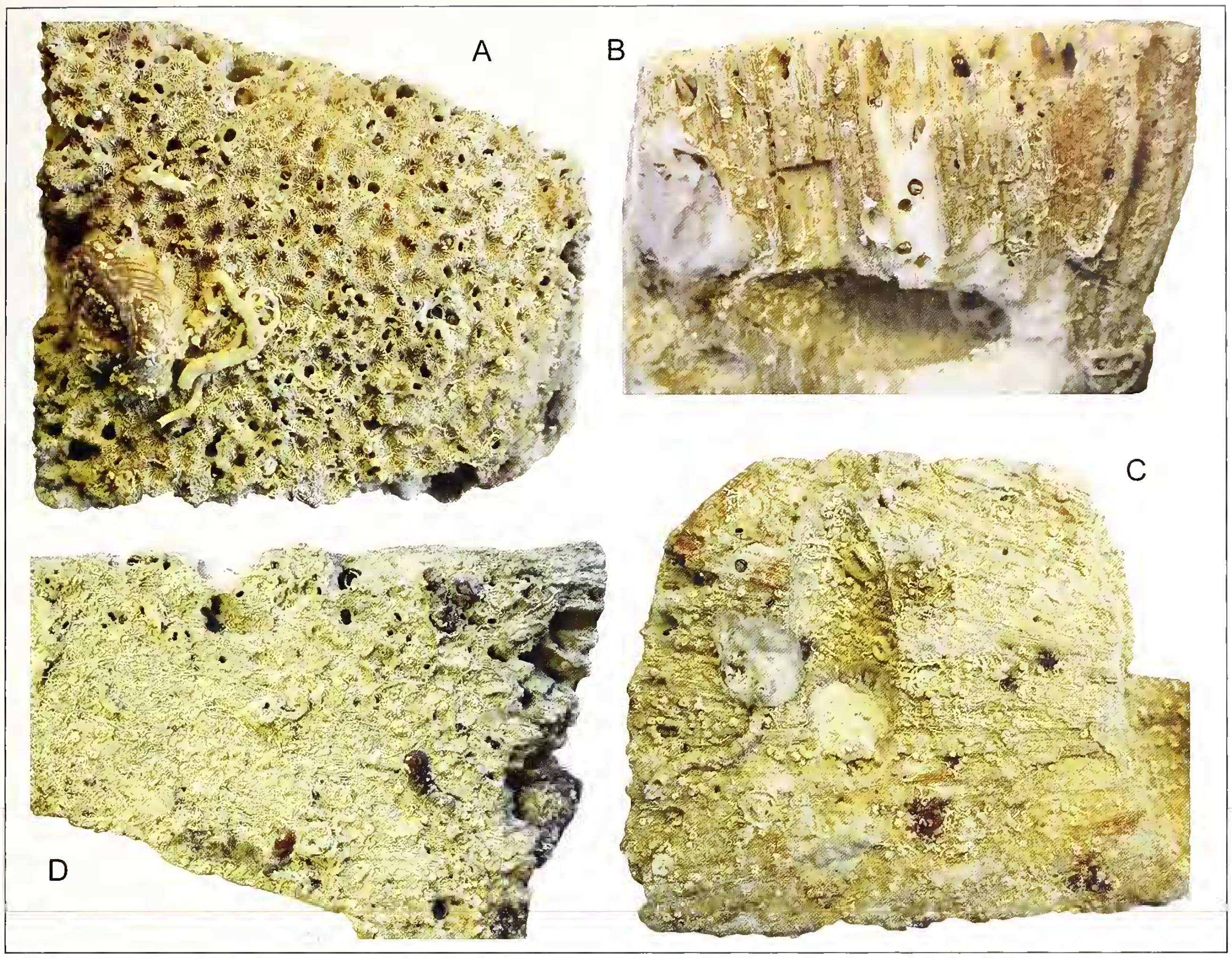

Fig. 5. *Siderastrea siderea*. **A**. Top view, slab thickness 6 cm. Many borehole orifices are irregularly dispersed over the surface. Some very small ones may stem from Oct. 1982 recruits, others were smothered by encrusters such as cirripeds, now removed. **B**. Above the longitudinally opened, big old borehole, note several minute orifices, dark dots, and a few small boreholes in cross-section, partly with remaining shells, of new recruits. They probably settled in Oct. 1982, close to the end of "summer" experiments. **C**. After "winter", the split surface had showed only two longitudinally opened, big boreholes, one in the middle and part of another at right, of inserted specimens. Now, the 7 x 6 cm area is densely covered by various polychaete tubes and a few orifices of bivalve borings, namely at the left. Recruits of oysters indicate this surface was the underside during the "summer" experiment. **D**. This side, cut not split, was in contact with the mesh-wire during "winter". Some of the smallest borehole orifices may belong to October 1982 recruits (see text). Note the strong bioerosion and bioaccretions by encrusters on the right edge. Photos K. Kleemann.

Fig. 5. *Siderastrea siderea*. **A**. Superficie superiore di una sezione spessa 6 cm. Sono presenti molte perforazioni irregolarmente distribuite. Alcune perforazioni molto piccole potrebbero risalire alla colonizzazione dell'Ottobre 1982, mentre altre sono state ricoperte da incrostanti, quali cirripedi, ora rimossi. **B**. Al di sopra della grossa perforazione sezionata longitudinalmente, si notano diverse piccole aperture, come puntini scuri, ed alcune piccole perforazioni sezionate, in parte ancora con conchiglie all'interno. Molto probabilmente esse risalgono all'Ottobre 1982, verso la fine dell'esperimento "estivo". **C**. Dopo l'esperimento "invernale" la superficie di frattura mostrava solo due ampie perforazioni, una al centro e parte dell'altra a destra dell'esemplare inserito sperimentalmente. Adesso, l'area di 7 x 6 cm è densamente ricoperta da tubi di policheti e sono presenti alcune perforazioni da bivalvi a sinistra. La colonizzazione da parte di ostriche indica che questa superficie era posizionata inferiormente durante l'esperimento "estivo". **D**. Questo lato, non spezzato ma sezionato, era in contatto con la rete durante l'esperimento "invernale". Alcune delle perforazioni più piccole potrebbero appartenere alla fase di Ottobre 1982 (si veda nel testo). Si noti l'intensa bioerosione ed il concrezionamento biologico sul margine destro. Foto K. Kleemann.

experiments on boring and growth rates. Shell length reached up to 21 mm after both periods. Considering the observed growth rate and a maximal shell length of about 38 mm, a local population succession rate of one to two years seems plausible (Kleemann, 1990).

The present findings of fast and intense bivalve settlement in newly exposed substrates are in contrast to several publications in which boring bivalves were reported either missing or to occur in small numbers only after one or more years. For example, they were missing after one year at the GBR (Tribolett et al., 2002), after two years at Moorea, French Polynesia (Chazottes et al., 1995). They occurred after two years at Aqaba, Red Sea (Hassan, 1998), after three years at the GBR (Kiene & Hutchings, 1994), as well as after two years at inshore, after four years at outer reef sites at the GBR (Osorno et al., 2005). As documented by these and comparative studies from three more sites at the GBR (Sammarco & Risk, 1990), boring bivalves seem to be a minor actor in bioerosion. Kiene (1985) found bivalves, *Gastrochaena* and *Lithophaga*, usually represented by only one or two borings in substrates after two to three years of exposure; none were identified after one year at Lizard Island, GBR.

Investigating the internal bioerosion of *Porites* across the Australian GBR, Sammarco & Risk (1990) noted a significant decrease with distance offshore; the abundance of bivalves and sponges decreased most significantly, and boring bivalves dominated inshore reefs. The latter can be explained by the fact that *Porites* is a well-known host of *L. (Leiosolenus) laevigata* (Kleemann, 1980, 1982, 1995). Although those authors did not mention the species or its association, the latter can be recognised by the numerous traces illustrated in an x-ray (Sammarco & Risk, 1990: fig. 5B), indicating successive bivalve generations in a sliced coral skeleton from Orpheus Island, only 14 km from shore. There, better nutrition than further offshore can be expected, as discussed above.

Musso (1993) investigated the skeletal degradation after death in three *Acropora* species at Lizard Island, GBR, Australia. Two of them, *cuneata* (Dana, 1846) and *brueggemanni* (Brook, 1893) are members of *Isopora*, a previous subgenus of *Acropora*, now in genus rank (Wallace et al., 2007). Being the host of *L. (Leiosolenus) kuehnelti* Kleemann, 1977, *Isopora* species may contain such bivalves (Kleemann, 1977, 1980, 1995). Unsurprisingly, Musso (1993) found bivalves in *I. cuneata* and *I. brueggemanni*, more in the former, a massive species, and less in the latter, being thin-branched (Kleemann, 1995: pl. 1, fig. 1). Those bivalves, however, were already present and killed together with the hosts at the beginning of Musso's experiments and did not develop during the experiments as suggested.

The factors that could influence the present results may include the size of the experimental substrates, the occurrence of inserted bivalves, the still living or decaying coral tissue on part of the slabs, and the protection by mesh-wire from larger predators such as fish and crabs. The shaded locality in the wreck probably reduced pressure from algal overgrowth, but not from various other space competitors, particularly from encrusting cirripeds and fast spreading oysters (**Fig. 6**). In principle, lithophagine specimens can keep their borehole openings free from lateral overgrowth using chelating secretions from the siphons as they widen the openings during bivalve growth. This is very well demonstrated in coral associates. To some extent, dead coral borers may be successful in preventing lateral overgrowth, if it is not too fast and compact. Veligers probably settle preferably on substrates already inhabited by con-specifics, which may be sensed chemically.

Substrate orientation – flat or steep, bright or shaded as on upper or lower sides of surfaces – and structural differences may influence colonisation patterns of boring bivalves. Note that the colonisation plasticity of *L. aristata* was recently investigated in south eastern Brazilian rocky shores. Lange et al. (2012) found this introduced species in highest densities of 100.0 ± 15.3 m^{-2} in 0.5 m at Guaíba Island, and 143.3 ± 26.1 m^{-2} in 3 m at Guaíba Terminal, Sepetiba Bay, in December 2005.

Astonishingly, the living surface of the first three prepared slabs survived the "winter" period and prevented veliger settlement. If the slabs would have been from Caribbean *Porites astroides* Lamarck, 1816, instead of *S. siderea*, veligers of *L. laevigata* would probably have settled as they do on their eastern Pacific hosts, *P. lobata* Dana, 1846, and *P. panamensis* Verrill, 1866. Glynn et al. (1972: p. 505) mentioned *L. (Leiosolenus) hancocki* Soot-Ryen, 1955 (a junior synonym of *laevigata*; Kleemann, 1980), from gut contents of triggerfish, *Balistes*. The Eastern Pacific appears to be unique in that many bivalves occur in the live part of corals (Highsmith, 1980). Highsmith et al. (1983) noted that lithophagine bivalves inhabiting *P. lobata* are three times more abundant in the upwelling enriched Gulf of Panama than in the adjacent but less productive Gulf of Chiriqui (mean 4220 versus 1350 m^{-2}) and that the bivalves grow approximately twice as fast in the former location. Scott et al. (1989) reported *P. lobata* inhabited by *L. laevigata* and *aristata* (but the latter infests only dead parts of live coral), with mean densities of 3060, 1870, and 480 m^{-2} of coral surface in Panama, Costa Rica and Galapagos, respectively. High densities were also noted in *Porites* colonies at Lizard Island, GBR (Kleemann, unpubl.). In the northern Red Sea, even denser populations were observed of three different *L. (Leiosolenus)* species associated with their host species of (1) *Montipora*, (2) *Cyphastrea* and *Echinopora*, and (3) *Stylocoeniella*, respectively (Kleemann, 2008). I corroborate the view of Highsmith (1981) that bioerosional damage to corals depends primarily on the amount of skeletal surface not covered by live tissue. I also support the view that species differences in mean skeletal excavation reflect differences in their ability to protect the skeleton from boring organisms by maintaining live tissue over it. Highsmith et al. (1983) mentioned that Glynn et al. (unpublished) had found boring bivalves more abundant in corals affected by upwelling than at less affected sites at Galapagos Islands. Highsmith (1980) had already found that bioerosion is positively correlated with plankton primary productivity because two major borers, bivalves and sponges, are planktivores. For the role of nutrient availability in bioerosion see also Hallock (1988, and references there-

Fig. 6. *Siderastrea siderea*. Underside of a re-exposed fragment, covered about half by oysters, up to 40 mm in diameter, further by polychaete tubes and cirripeds (some left over in the old, longitudinally split open boreholes). No new *Lithophaga* boreholes visible. Photo C. Baal.

Fig. 6. *Siderastrea siderea*. Superficie inferiore di un frammento riesposto, ricoperto per circa metà da ostriche, di dimensioni fino a 40 mm, oltre che da tubi di policheti e cirripedi (alcune all'interno di vecchie perforazioni sezionate longitudinalmente). Non è visibile alcun foro di recente formazione da parte di *Lithophaga*. Foto C. Baal.

Fig. 7. *Siderastrea siderea*. Traces of polychaete borings, 1.5 mm in cross-section, in coral fragment and a right valve of *L. aristata*. Note the septal structure of *S. siderea* corallites crossed by an old *aristata* boring. Photo K. Kleemann.

Fig. 7. *Siderastrea siderea*. Perforazioni da policheti con diametro di 1,5 mm in un frammento di colonia comprendente anche una valva destra di *L. aristata*. Si noti la struttura settata dei coralliti di *S. siderea*, messa a nudo da una vecchia perforazione di *L. aristata*. Foto K. Kleemann.

in). Comparing bivalve boring and growth rates of lithophagine bivalves in the Caribbean and Eastern Pacific corroborates these findings (Kleemann, 1990).

Conclusions

At Urabá Island, Taboga Islands, Panama, Eastern Pacific, large numbers of lithophagine veligers settled on coral slabs, metamorphosed to bivalves and bored into the substrates within days or at most in a few weeks. Surviving recruits of *L. aristata*, occurring in highest numbers, grew up to 16 mm in length during maximal 165 days in "winter" experiments. During "summer", recruitment was relatively low and had probably only started in October, before the end of experiments 1 Nov. 1982. The present results are in strong contrast to results from investigations of the succession of macro-borers in experimentally exposed coral substrates conducted at the GBR of Australia, French Polynesia and the northern Red Sea. In all these regions, boring bivalves were either missing or were observed only after years in the succession of settling organisms.

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